Butterflies of the California Channel Islands

Scott E. Miller

Santa Barbara Museum of Natural History, Santa Barbara, California 93105; Current address: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

Abstract. The butterflies (Lepidoptera: Papilionoidea and Hesperioidea) of the eight California Channel Islands are listed, with indication of residency status. Generally, the island faunas are depauperate aggregations of mainland species. The short geologic duration of isolation and high vagility of most of the species have limited endemism. A species/area relationship exists, but turnover in species composition over time (and thus MacArthur-Wilson equilibrium) is difficult to document with available data.

Introduction

The California Channel Islands are a group of eight continental islands, ranging in area from 2.6 to 249 km², located 20 to 98 km off the coast of southern California. This preliminary compilation includes butterfly data from recent fieldwork, museum collections, and the meager literature. Further fieldwork and analysis are necessary to complete knowledge of faunal composition and affinities. Fieldwork is difficult due to limited accessibility of several of the islands and island weather conditions, which include regular strong winds and dense fog.

The eight California Channel Islands (Fig. 1) fall naturally into two groups: four northern (San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands) and four southern (Santa Barbara, San Nicolas, Santa Catalina, and San Clemente Islands). During the Middle Pleistocene, most of the islands were submerged, and perhaps only Santa Catalina and the higher parts of Santa Cruz and Santa Rosa Islands remained above water (Johnson, 1978, 1983). During the Late Pleistocene, the northern islands were united into one large island by eustatically lowered sea levels. A Late Pleistocene land bridge to the northern islands has long been hypothesized, but neither geological nor biological evidence support a mainland connection since Early Pleistocene or before (Johnson, 1978). No connections existed among the southern islands during the Late Pleistocene. Therefore, the biotas of most of the islands have arisen since Middle Pleistocene times. For background information, see Miller (1984a), Miller and Menke (1981), and Power (1980).

Except for Santa Catalina Island, the islands have been surveyed for insects only by visiting entomologists. The butterflies of Santa Catalina



Fig. 1. California Channel Islands.

Island were treated by Meadows (1937, including description of Anthocharis cethura catalina), who lived on the island from 1927 to 1934. The only other island treatment is for Santa Cruz Island (Langston, 1981). Wright (1905) described the Santa Catalina Island endemic Strymon avalona (as Thecla avalona), and Ingham (1933) described Anthocharis sara gunderi from the same island. Emmel and Emmel (1975) described Euphydryas editha insularis, endemic to Santa Rosa Island. Other references to island butterflies include: Bowers (1890), Burns (1964), Cockerell (1938a, 1938b, 1939, 1940), Comstock and Dammers (1933), Coolidge (1923), Emmel and Emmel (1973), Evans (1955), Gall (1981), Goodpasture (1973), Gorelick (1971), Grinnell (1909), Hovanitz (1941, 1950, 1962), LeGare and Hovanitz (1952), Orsak (1976), Powell (1981, 1984), Remington (1971), Scott (1981), and Thorne (1970). Island butterflies are scattered throughout many collections; Principle sources of material are the Natural History Museum of Los Angeles County (LACM), Santa Barbara Museum of Natural History (SBMNH), California Insect Survey (University of California at Berkeley, CIS), and Peabody Museum of Natural History (Yale University); smaller amounts of material are in National Museum of Natural History (Smithsonian Institution, USNM), San Diego Natural History Museum, University of California at Davis, and other institutions.

Distribution Data

Table 1 lists the butterflies recorded from each of the islands, with

indication of the status of the island populations. Names generally follow Emmel and Emmel (1973). Resident (reproducing) populations are indicated by the abundance and quality of specimens, as well as records of immatures. Some species (e.g. Vanessa species) probably migrate regularly between the islands and the mainland, occasionally breeding, but not always maintaining permanent populations. See appendix for comments on taxonomic or residency status of some taxa.

Ecological Biogeography

Like most island organisms, the butterfly faunas of the California Channel Islands are depauperate compared to the adjacent mainland. Santa Cruz Island, with 34 species, has the largest butterfly fauna of the islands. This is less than half that of a region of equivalent area and elevational range on the adjacent coastal Santa Barbara region, which has about 70 resident butterfly species (Table 2). Possible reasons for this lack of island butterfly diversity include: (1) poor dispersal abilities of some butterflies due to limited vagility, (2) low habitat diversity and lack of or scattered, patchy presence of foodplants on the islands, (3) competitive displacement by other butterfly species, (4) physiological limitations of certain butterflies, and (5) destruction of original habitats by human activities.

Linear regression of number of species of butterflies against island areas yields a significant correlation (r=.83), with the following equation: species=7.3 + (.078) (area). Maximum elevation and number of plant species are also strongly correlated with number of butterfly species (Miller, ms). Butterfly numbers are remarkably similar to those of Orthoptera, the only other well surveyed group of insects on these islands (Table 3).

Many authors have used the existence of a species/area relationship to claim occurrence of MacArthur-Wilson equilibrium, This theory (MacArthur and Wilson, 1967) states that the number of species of a given higher taxon on an island is a function of rates of immigration and extinction, which in turn are dependent on area and isolation. However, demonstration of application of this model requires that (1) a relationship exists between number of species and area, (2) the number of species remains constant, and (3) the species present turnover with time due to extinction and immigration (Gilbert, 1980). Characterization of status of residency is difficult due to the problems in defining "colonization" and "extinction" (Simberloff, 1976), especially with the limited data available and the "weedy" nature of many of the species involved (which often have no "permanent" populations, but only ephemeral local "populations" which are regularly reestablished; Shapiro, 1982). Demonstration of turnover in California Island butterflies is difficult due to lack of adequate census data, especially over time.

In comparing Santa Catalina Island butterflies surveyed by Meadows (1937) from 1927-1934 with recent (1968-1981) collections (LACM, CIS, SBMNH), the number of species has remained approximately constant. During each period the apparent establishment or reestablishment of a species associated with cultivated plants has occurred: *Phoebis sennae* in 1928 and *Strymon melinus* (not restricted to cultivated plants) in 1978. Among other species, *Eurema nicippe* (associated with cultivated plants), *Danaus gilippus strigosus* (a migrant), and *Nymphalis californica* (a migrant) were taken only in the early period; *Junonia coenia* and *Plebejus acmon* only in the recent period. Thus some turnover may have taken place, but the breeding status of many of these species is not known and isolated populations could have been missed on this large, rugged island.

On Santa Cruz Island, although lack of data prevents comparisons of entire groups through time, Powell (1981) documented that an earwig, two moths and two butterflies not recorded in 1939-41 and 1966-69 surveys, became established during 1969-78. A third butterfly, Atalopedes campestris, is added herein (appendix). The earwig and moths were probably introduced by man, but the sudden appearance of the butterflies is not easily interpreted. They might have immigrated often during the 50-100 years Santa Cruz Island has had their weedy hostplants. Such species probably periodically colonize, are eliminated during stress such as overgrazing by feral sheep in drought years, then recolonize. Powell (1981, 1984) suggests that the insect faunas of the California Channel Islands, especially the badly perturbed ones, are undersaturated and have not yet established (or reestablished) equilibrium species numbers. Extinction presumably is (or has been) higher than normal, immigration lower, and/or colonization improbable due to reduced patch sizes of native hostplants.

The butterfly fauna of Santa Catalina Island is the best known of the California Islands due to the relative intensity of collecting there. The faunas of San Nicolas and San Clemente, both smaller and more isolated than Santa Catalina, are poorly known; isolation and limited habitat diversity are responsible for the small numbers of species, but the presently known faunas are undoubtly incomplete. The fauna of the tiny and isolated Santa Barbara Island appears to be fairly well known; this island has little habitat diversity and has suffered greatly from human disturbance (Philbrick, 1972). The fauna of Santa Cruz Island is well known, due especially to fieldwork by R. L. Langston, J. A. Powell, and C. L. Remington. The large size and topographic diversity of this island provides greater habitat diversity than any of the other islands. Anacapa Island (actually composed of three islets) appears to have a large fauna for its small size. This may be due to its proximity to both Santa Cruz Island and mainland sources of immigrants. The faunas of Santa Rosa and San Miguel Islands are poorly known due to incomplete collecting, but both are smaller and considerably less diverse in vegetation and topography than

Santa Cruz. Several of the islands, especially San Miguel, have suffered considerable overgrazing in the past (Johnson, 1980).

Historical Biogeography

Butterflies show little phenotypic endemism on the California Islands, although many individuals tend to be somewhat smaller and darker than those on the mainland, probably due largely to climatic factors (Hovanitz, 1941). Morphological variation in very few populations is significant and constant enough to warrant specific or subspecific status: Anthocharis sara gunderi, Anthocharis cethura catalina, Cercyonis sthenele new subspecies, Euphydryas editha insularis, Strymon avalona, and Ochlodes sylvanoides santacruza. Allozyme and karyotype frequencies of the fly Drosophila pseudoobscura Frolova from the California Islands do not differ much from those of mainland populations, indicating that isolation does not necessarily lead to genetic differentiation (Harshman and Taylor, 1978), although it can (Weissman, 1976).

Some butterfly populations on the islands differ considerably in phenology and/or abundance from mainland populations. On the islands Ochlodes sylvanoides flies from spring into summer (late April to August), apparently having shifted its later flight period on the mainland to replace that of Ochlodes agricola (Boisduval) which does not have insular populations; on the mainland, O. agricola flies in spring (May to June) at the same localities that O. sylvanoides occupies in the summer (June to September). The prolonged flight periods of several species are evidently due to the coastal climate with mild winters and cool summers (Langston, 1975) and reduced competition from related species which are absent on the islands. In one case, related species are found on adjacent islands but do not occur together: Euphydryas editha insularis is locally abundant on Santa Rosa Island and E. chalcedona is locally abundant on Santa Cruz Island, but neither island has both species.

Development of endemism has been limited by the high vagility of many species and the short geologic duration of isolation. Many of the island butterflies (e.g., Pieris protodice, P. rapae, Colias eurytheme, Vanessa atalanta rubria, V. cardui, V. annabella, V. virginiensis, Junonia coenia, Strymon melinus, Lycaena helloides, Brephidium exilis, Plebejus acmon acmon, Hylephila phyleus, Pyrgus albescens, and others) are common low-land colonizers elsewhere in California (e.g., Shapiro, 1975, 1980, 1982). The biotas of most of the California Islands must have arisen since the last submergence in the Middle Pleistocene (Johnson, 1978). The time since initial colonization (which may have taken place anytime since the last submergence) probably has not been long enough to allow significant morphological divergence on the islands. The fossil record is inadequate to document the morphological stability of butterflies during the Pleistocene (Shields, 1976) but the known Pleistocene butterflies (one papilionid, one

pierid, one nymphalid, and two hesperiids) are considered to be extant species (Zeuner, 1942, 1962; Fujiyama, 1968). Analysis of Pleistocene insect fossils, primarily beetles, from various Holarctic localities indicates great morphological stability of species from the Pleistocene through the present (Ashworth, 1979; Coope, 1979; Matthews, 1977; Miller, 1983). Furthermore, during the Late Pleistocene glaciations, the northern islands were united into one island (Johnson, 1978). For most butterflies, the duration of isolation on these islands has not been long enough to allow evolution of endemic taxa. Isolation has been limited by both geologic processes and vagility of the butterflies, some of which can easily cross the water barriers involved. Some of the island endemics may be relicts of taxa which were more widespread during the Pleistocene.

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Appendix. Notes on the taxonomic or residency status of certain island butterfly taxa.

Colias harfordii: The Santa Cruz Island specimens are assumed to be this, but the classification of mainland harfordii is still uncertain (e.g. Ferris, 1973; Klots, 1975). Eurema nicippe and Phoebis sennae: Once resident on Santa Catalina Island only at Avalon, where their introduced foodplant, Cassia species (Leguminosae), is cultivated (Meadows, 1937); no recent records.

Anthocharis cethura catalina: The restriction of the type locality to "ridge between Renton Mine and Jewfish Point at head of Pebbly Beach Canyon" by L. Miller and Brown (1981:75) is unnecessary since (as noted by Orsak, 1976) the holotype was collected at Grand Canyon and is so labelled.

Anthocharis sara gunderi: Although gunderi is considered a synonym of sara sara by some authors (Meadows, 1937; L. Miller & Brown, 1981), the Catalina population is as differentiated from sara sara as are the mainland sara subspecies (J.F. Emmel, pers. comm.). The Santa Rosa and Santa Cruz populations are, however, referable to sara sara.

Cercyonis sthenele: The Santa Cruz Island population is an undescribed endemic subspecies (C.L. Remington and J.F. Emmel, pers. comm.).

Agraulis vanillae incarnata: Occurs only where its introduced foodplant, Passiflora species (Passifloraceae), is cultivated on Santa Catalina Island (Powell, 1984). Euphydryas editha insularis: The subspecific characters, described (Emmel & Emmel, 1975) from six specimens collected in 1941, are consistent in a series collected at many localities on Santa Rosa Island in April 1976 (SBMNH).

Vanessa cardui: "A north-westerly flight of hundreds of specimens was observed on San Clemente between November 23 and 26, 1939. During the flight Dr. John Garth, on board the... Velero III, saw two specimens on the wing seven miles [11 km] off the northern end of the island" (D. Meadows, unpubl. notes at LACM).

Strymon melinus: Resident on all islands except Santa Catalina, where it evidently occsionally establishes temporary local populations (1918, 1978-1982).

Celastrina argiolus echo: Grinnell's (1909) record of "Cyaniris pseudoargiolus piasus" from San Clemente Island is probably this. Meadows (unpubl. notes) recorded echo from San Miguel Island, but since I have been unable to locate specimens, I consider this a misidentification of Everes amyntula.

Ochlodes sylvanoides: Scott (1981) has recently described the Santa Cruz Island population as O. sylvanoides santacruza, without consideration of other island populations. This name is unfortunate in view of the variability and taxonomic problems in Ochlodes (e.g. Tilden, 1975).

Atalopedes campestris: Three males collected in the Central Valley of Santa Cruz Island, in the field just west of the University of California Field Station, 22-29 June 1979 (C.D. Nagano: LACM), represent a new island record. Dornfield (1980:109) records the recent range expansion of this species into Oregon.

Erynnis funeralis: Burns (1964:133) suggested that Meadows' (1937:180) record of E. tristis from Santa Catalina Island actually applied to E. funeralis but had not seen the specimen. He has recently seen the specimen (and two others from Catalina, all in LACM) and confirms the funeralis identification (J.M. Burns, pers. comm.). The San Clemente Island record is based on 1 male collected at West Cove, 21 March 1972 (H.V. Daly: CIS).

Table 1. Butterflies of the California Channel Islands. Abbreviations: R=resident; I=resident, but dependent on introduced ornamental plants; S=stray (accidental occurrence); X=status undetermined (includes regular migrants).

	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island(s)	Santa Barbara Island	Santa Catalina Island	San Nicolas Island	San Clemente Island
DADIT TOMBAR	Š	ď	Š	Z	Š	Š	Š	Š
PAPILIONIDAE Papilio zelicaon Lucas Papilio eurymedon Lucas		X	R R			R		R
PIERIDAE								
Pieris protodice Boisduval & LeConte Pieris rapae (Linnaeus) Colias eurytheme Boisduval Colias harfordii Henry Edwards		R R	R R R	R	X X	R R R	R R	R X X
Eurema nicippe (Cramer) Phoebis sennae (Linnaeus) Anthocharis cethura catalina Meadows	S					I I R R		
Anthocharis sara gunderi Ingham Anthocharis sara sara Lucas		R	R			11		
NYMPHALIDAE								
Danaus plexippus (Linnaeus)		X	R	Χ	X	X		
Danaus gilippus strigosus (Bates) Cercyonis sthenele subspecies			R			S		
Agraulis vanillae incarnata (Riley)			R			I		
Speyeria callippe (Boisduval) Euphydryas c. chalcedona (Doubleday)			R					
Euphydryas editha insularis Emmel & Emmel		R						
Chlosyne gabbii (Behr)			R	R		-		
Nymphalis a. antiopa (Linnaeus) Nymphalis c. californica (Boisduval)		X	R			R S		
Vanessa atalanta rubria (Fruhstorfer)			R	X		R		

Vanessa cardui (Linnaeus) Vanessa annabella (Field)	X San Miguel Island	보 B Santa Rosa Island	공 공 Santa Cruz Island		XX Santa Barbara Island	공 Banta Catalina Island	X X San Nicolas Island	B B San Clemente Island
Vanessa virginiensis (Drury) Junonia coenia Huebner Adelpha bredowii californica (Butler) LYCAENIDAE		R X	R R R	R X		R R	X	R
Strymon avalona (Wright) Strymon melinus Huebner Satyrium s. saepium (Boisduval) Callophrys d. dumetorum (Boisduval) Lycaena helloides (Boisduval)	R	R	R R R	R	R	R X	R	R
Leptotes marina (Reakirt) Brephidium exilis (Boisduval) Everes a. amyntula (Boisduval) Plebejus a acmon (West. & Hewit.) Glaucopysche lygdamus australis Grinnell Celastrina argiolus echo (Edwards)	R R	R R R R	X R R R R	X R R R	R	R R R R	R R R	R X R
HESPERIIDAE Ochlodes sylvanoides (Boisduval) Atalopedes campestris (Boisduval) Polites s. sabuleti (Boisduval) Hylephila phyleus (Drury) Pyrgus albescens Ploetz	R X	X R R	R R R	R X	X	R R R	R	
Erynnis t. tristis (Boisduval) Erynnis funeralis (Scudder & Burgess)			R			X		X

Table 2. Butterflies of the Santa Barbara-Goleta coastal shelf and adjacent Santa Ynez Mountains, Santa Barbara County, California. Data from museum collections (especially Santa Barbara Museum of Natural History), private collections, and literature. Asterisk (*) indicates taxa not resident, or dependent on ornamental plants.

PAPILIONIDAE

Papilio zelicaon Lucas Papilio rutulus rutulus Lucas Papilio eurymedon Lucas

PIERIDAE

Pieris protodice Boisduval & LeConte Pieris rapae (Linnaeus) Colias eurytheme Boisduval Colias harfordii Hy. Edwards Colias eurydice Boisduval *Phoebis sennae marcellina (Cramer)

*Eureme nicippe (Cramer)
Nathalis iole Boisduval
Anthocharis sara sara Lucas
Anthocharis lanceolata australis
(Grinnell)

NYMPHALIDAE

Danaus plexippus (Linnaeus)

*Danaus gilippus strigosus (Bates) Coenonympha california california (Westwood)

Cercyonis sthenele (Boisduval)

*Agraulis vanillae incarnata (Riley)

Speyeria callippe (Boisduval)

Euphydryas chalcedona chalcedona (Doubleday)

Euphydryas editha (Boisduval)

Chlosyne gabbii (Behr)

Thessalia leanira (Felder & Felder)

Phyciodes pratensis pratensis (Behr)

[=P. c. campestris (Behr)]

Phyciodes mylitta mylitta (Edwards)

Polygonia satyrus satyrus (Edwards)

Nymphalis antiopa antiopa (Linnaeus)

(Boisduval)

Vanessa atalanta rubria (Fruhstorfer)

Vanessa cardui (Linnaeus)

Vanessa annabella (Field)

Vanessa virginiensis (Drury)

*Nymphalis californica californica

Junonia coenia Huebner Limenitis lorguini lorguini Boisduval

Limenitis bredowii californica (Butler)

LYCAENIDAE

Apodemia mormo virgulti (Behr) Calephelis nemesis californica McAlpine

Atlides halesus estesi Clench Strymon melinus Huebner Satyrium californica (Edwards)

Satyrium sylvinus dryope (Edwards) Satyrium auretorum spadix (Hy.

Edwards)

Satyrium tetra (Edwards)

Satyrium saepium saepium

(Boisduval)

Callophrys augustinus iroides (Boisduval)

(Boisdaval)

Callophrys dumetroum dumetorum
(Boisdaval)

Lycaena arota (Boisduval)

Lycaena gorgon (Boisduval)

Lycaena helloides (Boisduval)

Leptotes marina (Reakirt)

Brephidium exilis (Boisduval)

Everes amyntula amyntula

(Boisduval)

Plebejus acmon acmon (Westwood & Hewitson)

Euphilotes battoides bernardino
(Barnes & McDunnough)
Philotes sonorensis (Felder &
Felder)
Glaucopsyche lygdamus australis
Grinnell

Celastrina argiolus echo (Edwards)

HESPERIIDAE

Panoquina panoquinoides errans (Skinner) Lerodea eufala (Edwards) Paratrytone melane (Edwards) Ochlodes sylvanoides (Boisduval) Ochlodes agricola (Boisduval) Atalopedes campestris (Boisduval) Polites sabuleti (Boisduval) Hylephila phyleus (Drury) Pholisora catullus (Fabricius) Heliopetes ericetorum (Boisduval) Pyrgus albescens Ploetz Erynnis funeralis (Scudder & Burgess) Erynnis tristis tristis (Boisduval) Erynnis propertius (Scudder & Burgess)

Species recorded from the Santa Barbara area which are not residents or regular migrants:

PAPILIONIDAE

Papilio indra pergamus Hy. Edwards: The stated type locality, "near Santa Barbara" is evidently erroneous (Miller, 1984b).

Battus philenor hirsuta (Skinner): 1, Santa Barbara, 11 April 1911 (J.A. Comstock: LACM); 1, Carpinteria, 11 August 1956 (N.W. Baker: SBMNH).

PIERIDAE

Phoebis agarithe agarithe (Boisduval): 1 male, Santa Barbara, 19 April 1917 (T. Lehmann: SBMNH); cited by Emmel and Emmel (1973:21).

Euchloe ausonides (Lucas): 1 male, "Santa Barbara, July 1911" (LACM). The locality and date are probably both erroneous (P.A. Opler, pers. comm.).

NYMPHALIDAE

Speyeria coronis (Behr): The specimens Emmel and Emmel (1973:30) reported from "near San Marcos Pass" (1 each in SBMNH and LACM, not collected by Lane) appear to be mislabelled S. zerene (Boisduval) (L.P. Grey, pers. comm.), and are erroneous records.

LIBYTHEIDAE

Libythena bachmanii larvata (Strecker): 1 male, Carpinteria, 29 December 1963 (D. Davenport: SBMNH).

LYCAENIDAE

Hemiargus isola alce (Edwards): 2 females, Montecito, June 1960 (SBMNH).

HESPERIIDAE

Thorybes pylades (Scudder): 1 female, San Marcos Pass, 22 March 1931 (C.W. Kirkwood: Yale).

Table 3. Numerical data. Butterfly numbers from Table 1, excluding "stray" records and species feeding only on cultivated plants. Orthoptera numbers from Weissman and Rentz (1976) with corrections for recent changes (Rentz and Weissman, 1982; D.B. Weissman pers. comm. 1984).

ISLAND	AREA (km²)	BUTTERFLIES	ORTHOPTERA
San Miguel	37	6	8
Santa Rosa	217	20	26
Santa Cruz	249	34	40
Anacapa	2.9	15	14
Santa Barbara	2.6	8	8
Santa Catalina	194	24	32
San Nicolas	58	10	10
San Clemente	145	12	11